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The pinewood nematode - a warning for Europe

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Summary. The pinewood nematode (PWN), *Bursaphelenchus xylophilus*, the causal agent of the pine wilt disease (PWD), is recognised as a major forest pest threatening European pine forests and forestry industries. This nematode originated from North America spread first to Japan and then successively to other East Asian countries including China, Taiwan and Korea, and later to Portugal, Spain, and more recently to the Republic of Armenia and France. The primary hosts of PWN are coniferous *Pinus* species, including the European *P. pinaster* and *P. sylvestris*. The nematode is vectored by cerambycid beetles (*Monochamus* spp.). Spread of PWN has been exacerbated by climate change, with altered environmental conditions facilitating establishment and expansion of the nematode and its vector. Warm temperatures, increased droughts, and mild winters create favourable conditions for nematode reproduction, vector dispersion and enhanced tree susceptibility. Severe PWD symptoms are typically observed in regions where average summer temperatures exceed 20 °C. Current climatic shifts threaten forest ecosystems and timber industries in Europe. As climate change continues, increased areas of Europe are likely to be infected by PWN, and urgent adaptive management strategies will be required.

Keywords. *Bursaphelenchus xylophilus*, climate change, pine wilt disease.

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INTRODUCTION

Increased international trade has aggravated global dissemination of pathogens into new regions. Among these emerging threats, the nematode *Bursaphelenchus xylophilus* (Steiner and Bührer, 1934) Nickle, 1970, the pinewood nematode (PWN), is a damaging pest classified as an A2 quarantine pest by the European Plant Protection Organisation (EPPO). The nematode causes pine wilt disease (PWD), and is vectored mainly by *Monochamus* spp. (Coleoptera, Cerambycidae). The PWN affects coniferous trees and has been responsible for extensive economic and ecological losses in East Asia and Southern Europe. Climate warming is expected to exacerbate these losses, by increasing forest vulnerability and expanding environmental suitability for the nematode and its vectors.

The main objectives of the present review are: i) to provide an integrated and synthesis of current knowledge on PWN with particular emphasis on its biology, epidemiology, pathways of introduction, and projected distribution under climate change scenarios in Europe; ii) to analyse the role of climate change and of biotic interactions, host availability and vector presence, in determining the future risks of PWN establishment across Europe; and iii) to contribute to development of integrated, science-based approaches for preventing the PWN introduction, establishment, and spread, to help to safeguard resilience, productivity, and ecological integrity of pine-dominated forest ecosystems in Europe.

IDENTIFICATION AND DISTRIBUTION OF THE PINEWOOD NEMATODE, *BURSAPHELENCHUS XYLOPHILUS*

Bursaphelenchus xylophilus is a microscopic sexually dimorphic nematode with the general *Bursaphelenchus* characters. These include small and slender bodies, high cephalic regions offset by constrictions, having six lips, a well-developed stylet usually with weak basal knobs, a well-developed oval to quadrangular median bulb, and oesophageal glands overlapping the intestine (EPPO, 2026). *Bursaphelenchus xylophilus* diagnosis rely on observation of a set of distinctive specific morphological characters. Male specimens have ventrally curved tails with spicules ending in characteristic disc-shaped cuculli (Figure 1 A). Females have an anterior vulval lip which overlaps the posterior lip, forming a distinct vulval flap, and the tail tip is typically rounded (Figure 1 B). These diagnostic features are reliably expressed only in adults, as juveniles either lack them or display them in underdeveloped form. Accurate morphological identification of *B. xylophilus* and differentiation from other *Bursaphelenchus* species requires specialized expertise in nematode taxonomy (Braasch and Schönfeld, 2015), since this species shows considerable morphological overlap with other *Bursaphelenchus* species such as *B. mucronatus* (*B. m. mucronatus* Mamiya and Enda, 1979, and *B. m. kolymensis* Braasch, Gu and Burgermeister, 2011) also living in *Pinus* species in numerous European countries and also being transmitted by *Monochamus* insects. In some cases, molecular identification of *B. xylophilus* is mandatory (Braasch *et al*., 2011; Gu *et al*., 2011; EPPO, 2023).

This nematode is considered a native species to North America (EPPO, 2023). The first report of PWD symptoms was from Nagasaki, Japan in 1905. Despite the early discovery of trees displaying PWD symptoms, the causal agent remained unknown (Mamiya, 1988). In 1934, *B. xylophilus* was first described in the United States of America, as *Aphelenchoides xylophilus* Steiner and Bührer, 1934. It was later reclassified as *B. lignicolus* Mamiya and Kiyohara, 1972 after being identified as the agent responsible for the PWD in Japan. In 1981, Nickle *et al.* (1981) confirmed its designation as *B. xylophilus*. During the 1980s, PWN spread across Asia, being

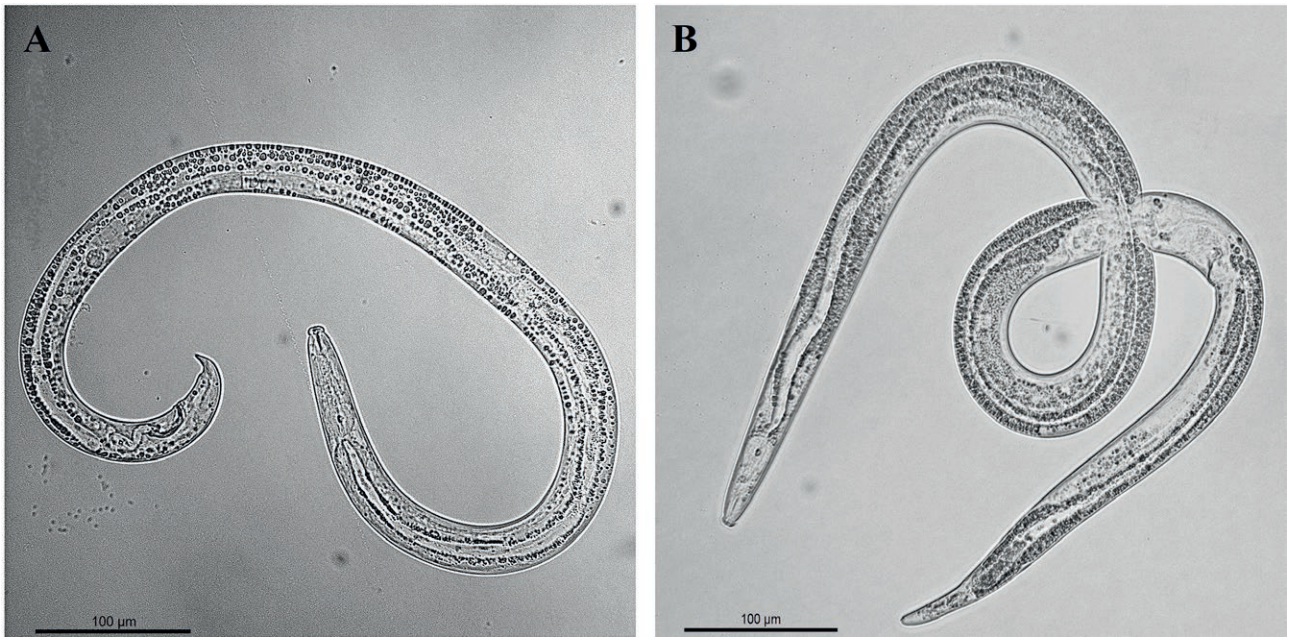

Figure 1. *Bursaphelenchus xylophilus.* (A) Male. (B) Female.

reported in China, Taiwan and South Korea in, respectively, 1982, 1985 and 1988 (EPPO, 2023). In Europe, the first occurrence of PWN was recorded in 1999 in *Pinus pinaster* Aiton (maritime pine), near Setúbal, mainland Portugal (Mota *et al*., 1999). Following this report, the EPPO classified PWN as an A2 quarantine pest (EPPO, 2023). Since this introduction, the nematode has spread throughout mainland Portugal (Figure 2 A). To prevent further dissemination to Europe, mainland Portugal was considered as an affected zone and a 20 km buffer zone was established along the Portuguese borders, where all conifers showing any wilting symptoms should be immediately removed (EU, 2012). In 2009, PWN was detected on Madeira Island, in *P. pinaster* (Fonseca *et al*., 2012). In mainland Portugal, the nematode has also been found in *P. nigra* J. F. Arnold (black pine) and *P. sylvestris* L. (Scots pine) (Inácio *et al*., 2015; Fonseca *et al*., 2024).

Despite containment measures, PWN was reported in Extremadura, Spain, in 2008, and this outbreak was officially declared eradicated in 2013, following the implementation of strict sanitation measures. Similarly, two other outbreaks were successfully eradicated, from Extremadura, and from Castilla y León. Spain currently has four active sites, corresponding to four demarcated zones (DZ), three of which are in the eradication phase (MAPA, 2024). In Spain, PWN has been reported in *P. pinaster* (Abelleira *et al*., 2011; Robertson *et al*., 2011), *P. radiata* D. Don (Monterey pine) (Zamora *et al*., 2015), and *P. sylvestris* (Díaz *et al*., 2025). More recently, PWN has also been reported in Republic of Armenia in *P. sylvestris* (Arbuzova *et al*., 2025) and in the south of France in *P. pinaster* (EPPO, 2025a) (Figure 2 A).

The vector species associated with *B. xylophilus* vary geographically. In North America, the primary vector is *M. carolinensis* Olivier, 1792; in Asia, it is *M. alternatus* Hope, 1842; and in Europe, it is *M. galloprovincialis* (Olivier, 1795) (Sousa *et al*., 2001; Jones *et al*., 2008; Akbulut and Stamps, 2011). At present, in Europe, only *M. galloprovincialis* has been confirmed as a vector of *B. xylophilus* (Sousa *et al*., 2001; Abelleira *et al*., 2020). However, there are other *Monochamus* species in Europe that are potential vectors, including *M. saltuarius* (Gebler, 1830), *M. urussovi* (Fisher, 1806), *M. sutor* (Linnaeus, 1758), and *M. sartor* (Fabricius, 1787) (Schröder *et al*., 2009; Naves *et al*., 2015; Pajares, 2016). *Monochamus saltuarius* and *M. urussovi* were confirmed as vectors of *B. xylophilus* in China (Li *et al*., 2020; Yu *et al*., 2026).

In Europe, *M. galloprovincialis* has a broad geographic range, being found across most of Europe except the United Kingdom and Ireland, and Belgium, Bulgaria and Norway (Figure 2B). This species is commonly detected in the Mediterranean basin, including France, Greece, Italy, Portugal, Spain, and Turkey. It has been found mainly associated with *P. pinaster*, *P. sylvestris*, *P. nigra* and *P. halepensis* Mill. (Aleppo pine) (Sousa *et al*., 2001; Naves *et al*., 2015; Abelleira *et al*., 2020; EPPO, 2025b). *Monochamus saltuarius* occurs throughout Russia and Eastern Europe, associated with *Picea* and *Larix* conifers. *Monochamus sartor* has been recorded in eastern and central Europe and in mountain forests in France, Italy, and Switzerland. The widely distributed *M. sutor* occurs from Scandinavia to the Alps and Pyrenees (Wallin *et al*., 2013; Naves *et al*., 2015).

Bursaphelenchus xylophilus has a large host range that includes conifer species of *Abies*, *Cedrus*, *Chamaecyparis*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga* (EPPO, 2023). Despite this diversity, species of *Pinus* are its primary hosts, and are widely distributed across the Northern Hemisphere.

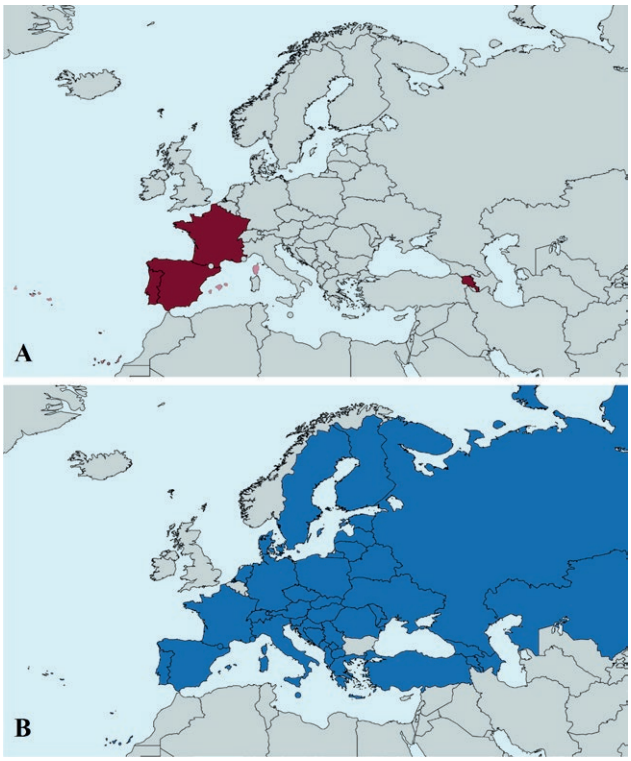

Figure 2. European geographical distributions of *Bursaphelenchus xylophilus* and its insect vector, *Monochamus galloprovincialis*. (A) Areas marked in dark red are countries where presence of *B. xylophilus* has been confirmed. (B) Areas marked in dark blue are countries where presence of *M. galloprovincialis* has been confirmed. *Bursaphelenchus xylophilus* and *M. galloprovincialis* distributions are based on data from the EPPO (EPPO 2025b; 2026). Maps were created using mapchart.net.

Host susceptibility differences within *Pinus* have been validated through laboratory pathogenicity studies, with nematode inoculations of pine seedlings. However, results obtained in these assays were variable, between pine species and within individual species. This emphasized how environmental conditions can influence pathogenic potential of nematodes (Silva *et al*., 2025).

Among the most important pine species in Europe, *P. sylvestris* and *P. pinaster* have been identified as the most susceptible to nematodes. *Pinus pinaster* has fragmented distribution within the Mediterranean basin, occurring along the Atlantic coast of the Iberian Peninsula, and in France and northern Italy. *Pinus sylvestris* is widely distributed throughout the European continent, especially in Central and Northern Europe (Figure 3).

European pine species of significant economic and ecological importance which are moderately susceptible to nematodes include *P. mugo* Turra (mountain pine), *P. nigra* and *P. halepensis*, while *P. pinea* L. (Stone pine) is considered the least susceptible (Evans *et al*., 1996; Fonseca *et al*., 2015; EPPO, 2026).

In susceptible species, PWN infections cause progressive decline, characterized by reduced resin exudation due to the rupture of resin canals, followed by yellowing and reddish browning of needles, and weakened branches in advanced stages. Symptoms usually appear approx. 3 weeks after infection, and tree mortality normally occurs within 1 to 3 months (Mamiya, 1980; Fukuda, 1997; Kuroda, 2008; Futai, 2013; Back *et al*., 2024).

THE LIFE CYCLE OF *BURSAPHELENCHUS XYLOPHILUS*

The PWN life cycle is complex, and different biological interactions occur involving three organisms: the nematode, the insect vector and the host tree (Figure 4).

The *B. xylophilus* life cycle consists of four propagative juvenile stages, two dispersive stages (formed under unfavourable conditions), and the adult stage (males and females). The first propagative juvenile stage (J1) develops inside egg during embryogenesis. After the first moult within the egg, the second propagative juvenile (J2) hatches, and then undergoes three subsequent moults to become J3, J4, and finally adults. The nematode completes its life cycle within 96 h and has high fecundity (24 eggs per female) (Mamiya and Enda, 1972; 1979; Mamiya, 1983). These features contribute to rapid population expansion.

The life cycle alternates between two phases: a phytophagous phase and a mycophagous phase. During the phytophagous phase, the nematodes feed on living pine tissues. In the mycophagous phase, they feed on fungi that colonize declining or dead host trees. When environmental conditions deteriorate, a specialized third dispersive juvenile stage (pre-dauer juvenile, JIII) is formed. These JIII nematodes aggregate near the pupal chambers of *Monochamus* spp. insect vectors, and moult into the fourth dispersive stage (dauer juvenile, JIV). The JIV nematodes are adapted for long-term survival and for dispersal via the insect vectors. When adult beetles emerge from their pupal chambers, the JIV enter

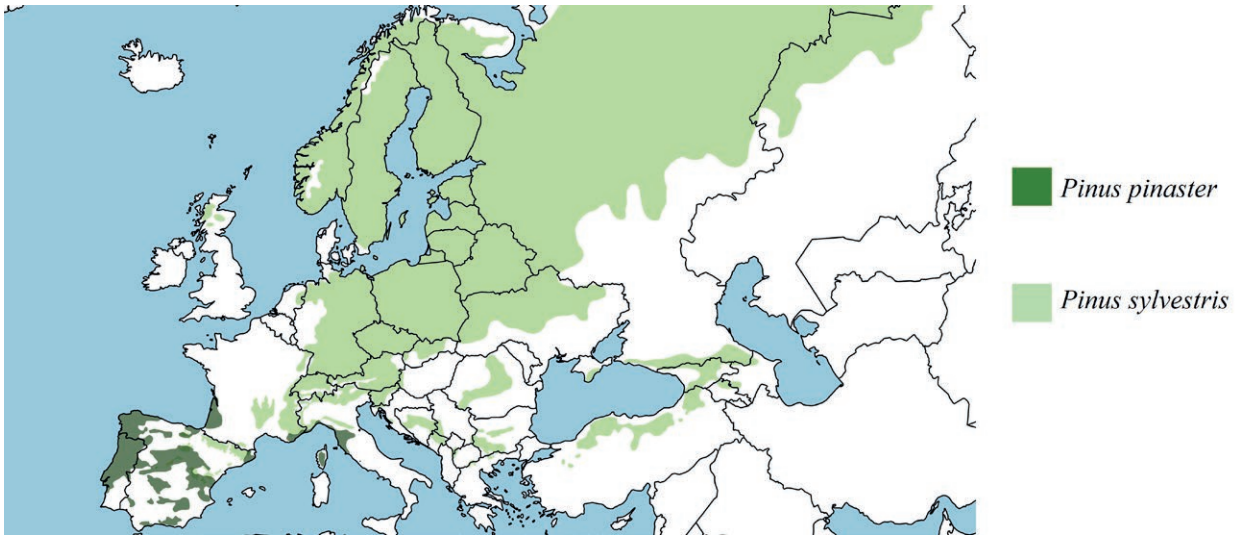

Figure 3. European geographical distributions of *Pinus pinaster* and *P. sylvestris* based on data from EUFORGEN (EUFORGEN, 2024a, b; Caudullo *et al*., 2026). The map was created using QGIS.org.

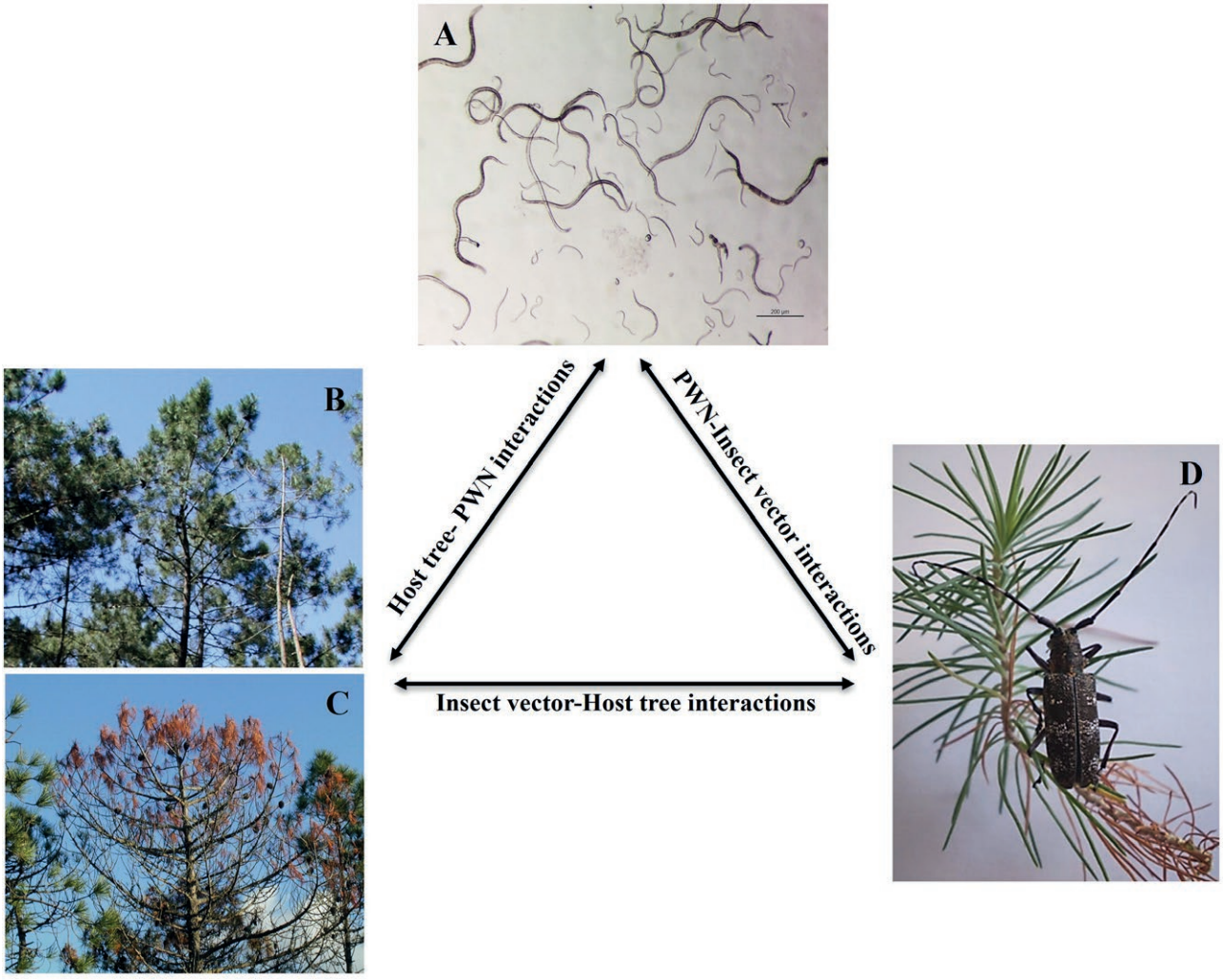

Figure 4. Biological interactions involved in pine wilt disease (PWD). (A) *Bursaphelenchus xylophilus* nematode suspension. (B) Healthy *Pinus pinaster* trees. (C) *P. pinaster* tree displaying PWD symptoms. (D). Insect vector, *Monochamus galloprovincialis.*

the beetle tracheal system, and are subsequently transported to new host trees. Transmission occurs either during beetle maturation feeding on healthy trees (primary transmission), or during oviposition on weakened or dead trees (secondary transmission). For secondary transmission, the nematodes feed on fungi colonizing the tree wood, completing the mycophagous cycle (Fonseca *et al.*, 2015; Cardoso *et al.*, 2024; Silva *et al.*, 2025; EPPO, 2026).

In primary transmission, most JIV individuals penetrate susceptible trees, and then moult into adults. These then reproduce and spread through host plant vascular systems (phloem and xylem), invading the conductive vessels (tracheids and vessel elements) that are responsible for transporting raw sap (water and minerals). The feeding activity of the nematodes on parenchyma and epithelial cells of the tree resin canals causes cavitation and embolism in the tracheids, blocking sap flow and leading to gradual reduction in resin production until it ceases. When temperatures exceed 20 °C, foliar transpiration ceases within 20 to 30 d after infection, and symptoms of needle discolouration, leaf wilting, and tree death may appear 2 to 3 months later (Kiyohara *et al.*, 1975; Mamiya, 1983; Kuroda, 2008; Futai, 2013; Silva *et al.*, 2025; EPPO, 2026). Ability of *B. xylophilus* to switch between vector species enables the nematode to establish in new regions regardless of the specific vector present, as the mode of transmission remains consistent among *Monochamus* species (Kanzaki and Giblin-Davis, 2018). The risk of spread to European countries has created urgent need for development of tools that can be used to detect and monitor the nematode and the insect vectors.

PROJECTED DISTRIBUTION OF *BURSAPHELENCHUS XYLOPHILUS,* AND EXPECTED DAMAGE IN EUROPE UNDER CLIMATE CHANGE SCENARIOS

Climate change can profoundly influence species distributions, phenologies, and physiological processes. Species persistence under changing climatic conditions may occur through phenotypic plasticity, evolutionary adaptation, or shifts to habitats with favourable climates (Trisos *et al*., 2020). In the case of the PWN, there is evidence that in some regions it can persist at low population densities without causing noticeable host plant damage, as was reported in Republic of Armenia, where over 2 years of investigation, only six individuals (three males and three females) were identified (Arbuzova *et al*., 2025). This suggests that PWN may be more widely distributed than is currently recognized, remaining latent and causing no significant symptoms until environmental conditions become favourable for population increase and disease expression. This possibility requires further consideration when assessing the potential risks and future spread of the nematode.

As a quarantine organism within the European Union, *B. xylophilus* is subject to strict surveillance and containment measures that are enforced through national action plans and port-of-entry inspections. National Plant Protection Organizations and border control agencies are responsible for implementing phytosanitary regulations while maintaining trade flows. Transport of infected wood or related products such as wood packaging material (WPM) represents the main pathway for long-distance PWN dissemination (national or international). Logs, pallets or untreated wood products can contain nematodes and insect larvae and/or pupae, enabling the PWN introduction into non-infected areas. Once introduced, the presence of susceptible hosts and local *Monochamus* species facilitate PWN establishment and spread (Figure 5).

To mitigate these risks, wood and WPM used in international trade must undergo approved phytosanitary treatments and PWN detection procedures in the wood, the WPM, and in forest areas.

Accurate identification of *B. xylophilus* is essential for effective forest management, and to avoid the PWN dissemination to non-infected areas. Traditional identification relies on morphological diagnostic characters of adults, mainly the shape of male nematode spicules, the female vulval region, and tail morphology (EPPO, 2023). Due to intra-specific morphological variations in some PWN isolates it is difficult to identify PWN based only on morphological characters. In these cases, molecular methods must be implemented (EPPO, 2023; Silva *et al*., 2025). To mitigate these risks, wood, bark and WPM used in international trade must undergo approved phytosanitary treatments.

Figure 5. Schematic representation of establishment and spread of the pinewood nematode (PWN), *Bursaphelenchus xylophilus*, into new geographical areas.

International Standards for Phytosanitary Measures (ISPMs), developed under the International Plant Protection Convention (IPPC), provide a harmonized framework for global biosecurity. ISPM 15 specifies treatments and marking requirements for WPM. Within the ISPM 15, all WPM must be subjected to appropriate treatments, including heat treatment (HT), microwave dielectric heating (DH), or fumigations with either methyl bromide (MB) (restricted in Europe) or sulfuryl fluoride (SF). The HT is the most widely adopted method to eliminate forestry pests and is implemented in industrial heat chambers with the requirement that all wood (including in the core) reaches a minimum of 56°C for a minimum 30 continuous minutes. All WPM entering the EU is subject to inspection, and any evidence of pest activity triggers sampling and laboratory verification of treatment efficacy (IPPC, 2021). For bark treatment, a thermal treatment was developed in Portugal, that involves application of saturated steam at temperatures ≥100 °C. Material to be treated is conveyed through a thermally insulated chamber, and all bark material must reach a minimum of 64 °C for at least 30 consecutive minutes (IPQ, 2023).

Despite the phytosanitary measures implemented in Europe, documented interceptions of *B. xylophilus* remain limited but recurrent. The nematode was detected in Finland in 1984, 1990 and 1992, in wood chips and sawn wood consignments originating from Canada and the United States of America (EPPO, 1984, 1990, 1992a).

In 1988, it was also detected in Sweden in wood chips from Canada. In 1991, infected pine boards from Canada were intercepted in Finland (Tomminen, 1991), and in 1992 kiln-dried infected wood originating from Canada was intercepted in France (EPPO, 1992b). In 2011, *B. xylophilus* was intercepted in Switzerland in coniferous bark from Portugal (EPPO, 2011), and in 2018 was detected in France, while transiting through Belgium, in bark sourced from Portugal (DGAL, 2018). In addition to nematode interceptions, movement of insect vectors also represents significant pathways of introduction. Between 1998 and 2020, more than 100 interception records of *Monochamus* spp. on wood packaging material were reported within the European Union (EFSA, 2018, 2020). Collectively, these records highlight the persistent risk of introduction of *B. xylophilus* and its vectors into European countries, despite the implementation of regulatory and phytosanitary measures.

Strengthening surveillance at high-risk entry points remains essential, particularly given the difficulty of nematode and vector detection and the limited effectiveness of eradication following establishment. Even in cool northern regions where PWD symptoms may not develop, presence of PWN can result in severe trade restrictions. Although ISPM 15 mandates heat treatment, interceptions of PWN and *Monochamus* spp. continue to be reported. Simulations of potential introductions across 200 major European ports identified Eastern and Northern Europe, principally Bulgaria, Croatia, Greece, Hungary, Italy, Romania, Slovakia, Slovenia, and Ukraine, as critical monitoring points. In contrast, additional introductions in Spain or southern France would pose limited incremental risks by 2030 if containment in Portugal were to fail, emphasizing the strategic importance of eastern European ports (Robinet *et al*., 2011).

Climate strongly influences PWD, with temperature and drought affecting nematode multiplication, vector activity, and host susceptibility and symptom expression (Rutherford and Webster, 1987; Naves and Sousa, 2009; Estay *et al*., 2014; Gruffudd *et al*., 2016; Estorninho *et al*., 2022). Significant disease incidence typically occurs where mean summer temperatures (MST) exceed 19 to 20 °C, while mean annual temperatures (MAT) < 14 °C are associated with delayed disease expression (Gruffudd *et al*., 2016). Projected climatic changes, including rising temperatures, altered precipitation, and more frequent extreme events, are expected to increase forest vulnerability and expand the potential range of PWN and its insect vectors.

Experimental and modelling studies indicate that PWN development and fecundity increase with temperature between 10 and 35 °C, with optimum growth occurring at 25 to 31 °C, although extreme temperatures may reduce survival (Zhang and Cai, 2007; Pimentel and Ayres, 2018; Yoon *et al*., 2023; Aierken *et al*., 2024). High temperatures intensify transpiration in pine trees, causing rapid water loss and limited uptake of water and nutrients. This physiological stress weakens the trees, increasing their susceptibility to PWN infections and the development of PWD (Roques *et al*., 2015; Yamaguchi *et al*., 2020; Aierken *et al*., 2024). The relationship between temperature and PWD incidence follows an inverted U-shaped pattern. As temperature increases, PWD incidence increases until reaching a peak at a threshold temperature. Beyond that point, incidence of the disease declines with further increases in temperature. The threshold temperature shows spatial heterogeneity and is associated with local average temperatures (Zhang *et al*., 2025). Although increased precipitation can alleviate drought stress and slightly reduce PWD incidence, its effect is relatively minor compared with that of elevated summer temperatures (Hao *et al*., 2022; Aierken *et al*., 2024). Results obtained by Zou *et al*. (2024) also indicated that occurrence of PWN is associated with precipitation below 3000 mm in the warmest annual quarter, suggesting that areas where pines experience water stress may be at higher risk of PWN invasions.

Vector biology further amplifies climate-related risks. The development rate of *M. galloprovincialis*, the primary European vector, increases linearly between 15 and 30 °C (Ziter *et al*., 2012; Roques *et al*., 2015). Increased temperatures are therefore likely to expand vector ranges and accelerate their life cycles, increasing opportunities for nematode transmission (Roques *et al*., 2015). Nevertheless, when temperatures exceed 30 °C, developmental rate of *M. galloprovincialis* decreases significantly, with a lethal upper threshold for the nematode considered to be between 32 and 35 °C (Naves and Sousa, 2009).

Host plant species distributions are also projected to shift with climate change. Species distribution models predict substantial increases in suitable habitats for PWN-associated pine species across Europe (Xiao *et al*., 2024). While temperature predominantly governs host plant distribution, precipitation-related variables, such as precipitation seasonality and precipitation during the warmest annual quarter; also play important roles (Tang *et al*., 2021). Combined water deficits and elevated temperatures increase host susceptibility (Hirata *et al*., 2017). Consequently, climatic suitability for PWN is expected to increase in central and northern Europe, whereas Mediterranean regions may retain nematode-favourable climates but experience declining host suitability (Xiao *et al*., 2024).

Process-based models further illustrate the ecological consequences of PWN introductions. Simulations have projected 62.8 to 90.0% pine mortality over a 100-year period in Central Europe, accompanied by annual forest carbon losses of up to 5.6% (Schafstall *et al*., 2024). In the Iberian Peninsula, long-term modelling has predicted gradual colonization by the nematode of nearly all pine forests, including the Pyrenees, at an average rate of 0.83% per year, with climate imposing limited constraints on nematode spread (De la Fuente *et al*., 2018; De la Fuente and Saura, 2021).

Several climate-based risk assessments have also indicated shifting vulnerability of pine hosts across Europe. For example, in Germany, extreme heat events, such as the 2003 heatwave, could trigger disease expression, with future IPCC scenarios projecting increased susceptibility in northeastern regions where *P. sylvestris* is present (Gruffudd *et al*., 2016, 2019). In Finland, current and projected climates are considered unsuitable for PWN establishment, except under an extreme scenario by 2080, indicating a potential need to reassess long-term biosecurity priorities (Tuomola *et al*., 2021). Internationally, a 3 °C temperature increase could expand PWD-suitable areas in China by up to 40%, with comparable trends also anticipated in Europe (Robinet *et al*., 2011).

The economic consequences of uncontrolled PWN spread are substantial. Partial equilibrium analyses have estimated that by 2030, PWN could affect 10.6% of the assessed EU forest area, resulting in cumulative wood losses valuing approx. €22 billion over 22 years, and social welfare losses exceeding €218 million (Soliman *et al*., 2012).

Incorporating species interactions into PWN projections improves estimates of potential distributions compared to climate-only models. By incorporating species interactions, it becomes possible to predict accurate potential distribution of the PWN, which may be overlooked by climate-only models. Biotic interaction models show overall increases in suitability for PWD under future climate scenarios. Relative to nematode-only models, biotic models predict increased international suitability as climates become increasingly favourable for host–vector complexes, revealing that PWN could spread into new regions where suitable hosts and vectors coexist. These findings underscore the necessity for integration of biotic interactions into species distribution modelling, to avoid underestimating future disease risks. Including vectors and hosts in the PWN model gave an increased pessimistic view of the future of PWD compared to modelling the nematode alone (Zou *et al*., 2024). Thus, climate warming will likely expand the ranges of the vectors and accelerate their development rates (Roques *et al*., 2015), and consequently the affected regions may become high-risk for invasions of the nematode. In addition to temperature-related bioclimatic variables, precipitation seasonality and precipitation during warmest annual quarters are also important variables for host plants and vectors (Estay *et al*., 2014; Hirata *et al*., 2017). Water deficits combined with high temperatures increased tree susceptibility, with rising temperatures negatively affecting forest growth through aridification of regions where droughts can constrain the growth and productivity of pine trees (Martínez-Vilalta et al., 2008; Hirata *et al*., 2017). The host complex will suffer decreases in suitable areas under climate change scenarios. This may increase nematode invasion risks, and warmer summer temperatures are thus likely to trigger PWD expression in new areas.

In infected areas, carbon losses attributed to *B. xylophilus* have exceeded those caused by wildfires, regarded as key driver of forest disturbances. Environmental variables indicate that the predicted northward shift in precipitation will intensify *B. xylophilus* spread, placing 78% of Eurasia's boreal forests at risk by 2100. Among these high-risk areas, 62% contribute significantly to the world carbon sink. If current trends persist, carbon losses caused by PWD could exceed 39% of the total carbon stored in terrestrial ecosystems (Zhou *et al*., 2024).

Most projections indicate that regions currently limited by low temperatures (Centre and North of Europe) may become increasingly vulnerable to PWD, while areas already affected could experience increased disease pressure and rapid spread. Climate changes influence development and spread of PWN through interconnected effects on host trees, insect vectors, and the PWN. Increased temperatures, increased drought, and more frequent extreme climatic events will intensify physiological stress in pine hosts, reducing their defensive capacity and increasing susceptibility to pathogen infection. Warm conditions also enhance survival, activity, and dispersal of *Monochamus* spp. Once introduced into stressed host trees, the nematode rapidly reproduces within the xylem and resin canals, obstructing water transport and leading to wilting and eventually to tree death. Infected and dead trees then serve as reservoirs for further vector infestations, facilitating local disease increase and reinforcing feedback loops that accelerate the expansion of PWN under changing climatic conditions (Figure 6).

CONCLUSIONS

Introduction and spread of *B. xylophilus* continue to pose serious threats to forest health, driven by the com-

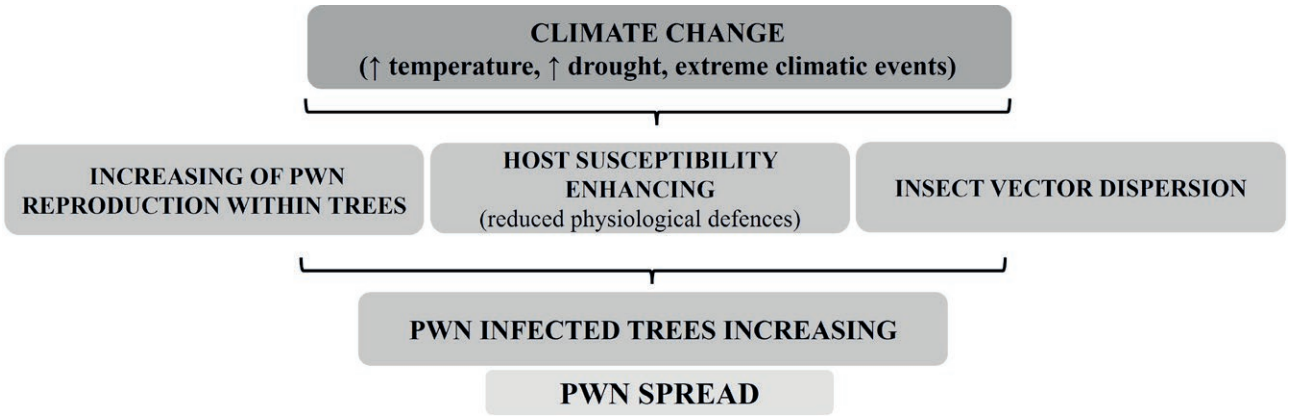

Figure 6. Schematic representation of the effects of climate change on the spread of the pinewood nematode (PWN), *Bursaphelenchus xylophilus*.

bined effects of climate change, international trade, and biological traits of the nematode and its insect vectors. High-risk pathways, such as untreated wood packaging material, raw timber, and plants for planting, facilitate long-distance dispersal, while favourable climatic conditions and widespread host availability increase the probability of establishment of the nematode in the EPPO region. Experience from affected areas, notably Portugal, demonstrate that eradication of *B. xylophilus* after establishment is difficult and costly, emphasizing the importance of preventive measures along entire wood production and trading sequences.

Climate warming is expected to exacerbate these risks by increasing forest vulnerability and expanding environmental suitability for *B. xylophilus* and its vectors. Although frequent interceptions confirm the high dispersal potential of this nematode, establishment is not always successful, highlighting persistent knowledge gaps regarding the ecological, physiological, and epidemiological processes underlying invasion success. Improved understanding of nematode–host–vector interactions, and their environmental constraints, is therefore essential for development of effective management strategies.

Biotic models, which incorporate host and vector distributions, predict broader future suitability for PWD than nematode-only models. This suggests that climate change may enhance the suitability of vector–host complexes, enabling disease spread into new regions (such as Central and Northern Europe) where these components coexist.

Effective long-term management of PWN will depend on integrated strategies combining prevention, early detection (annual monitoring), enhanced diagnostics, identification of risk areas, advances in remote sensing technology and artificial intelligence, development of resistant host through plant breeding, and strengthened international collaboration. These strategies could be utilized to precisely identify and monitor infected trees, aiding disease control. Aligning knowledge advances with phytosanitary policy and sustainable forest management practices remains essential to mitigate the impacts of *B. xylophilus*, and to preserve the resilience and ecological integrity of all pine-dominated forest ecosystems.

AUTHORS CONTRIBUTIONS

Luís Fonseca and Isabel Abrantes: conceptualization, writing of the original draft, writing review and editing, and funding acquisition.

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